Simulated climate change in dry habitats: do spiders respond to experimental small-scale drought?

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Abstract. Ground invertebrates such as spiders react to changing conditions in their terrestrial environments. Due to climate change, changes of species diversity, community composition and ecological traits (e.g., habitat specialization) can be assumed. Since it is often impossible or impracticable to carry out large-scale investigations concerning the impact of microclimate change on soil arthropods, studies on responses of arthropod communities to simulated climate change at a smaller scale may be a useful alternative. I conducted a field experiment to detect potential changes in species richness, community structure and ecological traits of spiders caused by prolonged drought. In a semi-dry grassland/*Juniperus communis* heath complex, five 16-m² plots were subjected to either a drought (excluding all rain) or non-drought treatment. Activity densities of spiders were measured using pitfall traps from July to September, 2008. Although differences in microclimate between treatments were significant, no significant treatment effect on either species richness or activity densities was found. Ordination analyses (NMDS) and multivariate analysis of variance (MANOVA) revealed no significant difference in assemblage composition between the treatments, nor were any changes in ecological traits detected. Spiders were not a suitable model group for detecting any changes in the present study, but comparable experiments yielded changes for at least some spider families and especially for microarthropods. For future small-scale studies I recommend a multi-species group approach with micro- and macroarthropods, using a broad spectrum of sampling techniques.

Keywords: Araneae, dry grassland, global change, heathland, suboceanic climate

Due to global climatic change, microclimate and soil conditions in some places are dramatically changing (Spekat et al. 2006; IPCC 2007). Since most soil invertebrates, such as spiders, react to changing conditions in their terrestrial environments (Frampton et al. 2000; Lindberg et al. 2002; Whitehouse et al. 2002; Lensing et al. 2005), changes in invertebrate diversity, community structure and ecological traits can be expected.

Merkens (2002) stated that the present Atlantic climate of Northwest Germany reduces the extreme character of dry habitats, making them more suitable for habitat generalists. Thus, habitat generalists are very abundant in dry grasslands and heathlands of this area (Merkens 2002; Buchholz 2008; Buchholz & Hartmann 2008). But, as climate changes, species composition should change toward a dominance of droughtresistant habitat specialists that can cope with more extreme microclimatic conditions. Simultaneously, drought-sensitive habitat generalists should decline. Apart from shifts in habitat preferences, further changes in ecological traits due to warming might be detected. For example, since dry and warm habitat conditions favor large-bodied spiders, the proportion of small-bodied species should decrease (Remmert 1981; Entling et al. 2009).

Hence, it seems worthwhile to study responses of soil invertebrates to changes in microclimate. It has already been proven that spiders are a suitable model group to detect such changes. Changes in moisture have direct effects (Dondale & Binns 1977; Rushton et al. 1987; Frampton et al. 2000; Wagner et al. 2003), or in the case of changes in habitat structure, an indirect impact on spider populations (Ward & Lubin 1993; Foelix 1996). Because it is often impossible or at least impracticable to carry out investigations of responses to changing microclimate at a larger scale, studies of small-scale responses of arthropod communities to simulated climate change may provide a useful alternative (Greenslade 1981; Whitford 1992; Hodkinson et al. 1998; Lensing et al. 2005; Lensing & Wise 2006). Thus, the aim of the present study is to investigate spider responses to microclimatic ehanges by focusing on the following hypotheses:

- 1) Increased drought will reduce species richness and activity density of particular species.
- 2) The spider community structure will change due to increased drought.
- 3) The average niche position of the spider community for moisture will shift to more dry and warm conditions (decreasing moisture preference), and the niche width will be reduced (increasing habitat specialization; e.g., number of xerothermophilic species).
- 4) Species will on average be larger in the drought plots.

METHODS

Study site.—The study was performed in a semi-dry grassland/*Juniperus communis* heath complex with the following vegetation structure (mean \pm SD): coverage of herbal layer ($20 \pm 9\%$), moss ($40 \pm 30\%$), litter ($10 \pm 5\%$), bare ground ($40 \pm 30\%$), height of herbal layer (10 ± 1.5 cm). The site was located near Münster ($51^{\circ}57'46.6''N$, $7^{\circ}37'43.3''E$) in North Rhine-Westphalia, Germany. The climate in this region is suboceanic, with an average annual temperature of 7.9° C and an average annual precipitation of 758 mm (Murl NRW 1989). During the investigation period (July–September 2008) the mean daily temperature was 16.5° C (mean minimum = 12.7° C, mean maximum = 20.7° C). Total rainfall was 42 mm (meteorological station of the Institute of Landscape Ecology, University of Münster).

Study design and sampling.—Five 16-m² unfenced plots were each subjected to a drought treatment (drought plots excluding all rain) or a non-drought treatment (control plots), respectively. Thus two treatments were compared with five replicates each. The five treatment pairs (drought/control plot,

side by side) were located randomly in the study site, keeping a minimum distance of 10 m between each other and from Juniperus stands. Rainout shelters were placed over the five drought plots on 28 June 2008. The roofs (wooden frame, transparent plastic cover - polyethylene, 0.2 mm thick) were positioned with a slope above each drought plot so that the height on the outside was 60 cm and 80 cm in the middle. The slope ensured that water would immediately flow off the roof. On 11 July 2008 a circle of four pitfall traps (diameter 9 cm, 10 cm apart, filled with a 4% formalin-detergent solution) were installed around the center of each plot. Afterward they were emptied every two weeks until 5 October 2008. The catches were transferred to 75% ethanol, and adult spiders were identified to species level using Roberts (1987, 1998) and Nentwig et al. (2003). The nomenclature follows Platnick (2008).

To compare microclimatic conditions in drought and control plots, air temperature and air humidity were measured once per hour 10 cm above the soil surface in the center of each plot with a data logger (Fourier Systems: MicroLog EC 650 including external temperature sensor). Precipitation data were taken from the Münster meteorological station (Institute of Landscape Ecology, ca. 12 km from the study area).

Statistical analyses.—Species richness was calculated as the number of species per treatment unit (McCune & Grace 2002). Three ecological traits were chosen to investigate responses to treatment: moisture niche position, niche width (Entling et al. 2007) and body size. Niche position values range from 0 to 1, where low values indicate a preference for moist habitats (niche position is 0 for species that prefer the moistest habitats). Low values for niche width include a narrow niche and high habitat specialization. Roberts (1987, 1998) was consulted for the average body sizes of spiders. For all subsequent analyses mean values of females were used.

All statistical analyses were done using the free software environment R 2.9.0 (R Development Core Team 2009) including packages VEGAN (Oksanen et al. 2008) and MASS (Ripley 2008) for multivariate statistics. Prior to the analyses of differences in microclimate and ecological traits between treatments, variables were tested for normal distribution using the Shapiro-Wilk test. If normal distribution of data was not met (even with transformed data) Wilcoxon rank tests were applied. In case of normal distribution, *t*-tests were applied. To detect possible responses of species richness and species activity to increased drought, generalised linear models (GLM) were used. To compensate for overdispersion, standard errors were corrected using a quasi-Poisson model (Crawley 2008; Zuur et al. 2009). Treatments (drought, control) were chosen as predictors for species richness (number of species), total counts of individuals, adults and juveniles.

To analyse differences in species distribution between drought and control plots non-metric multidimensional scaling (NMDS) was used. For ordination, the abundances of each species were square-root transformed and standardized (individual sums/number of sampling days/number of pitfall traps).

Vagrant species that occurred with only one individual per plot were omitted from the analyses to minimize their influence. Altogether, counts of 25 species were subjected to the ordination. For further statistical background about NMDS see Clarke (1993) and McCune & Grace (2002). A maximum of 20 random starts was used in search of a stable two-dimensional ordination model. A multivariate analysis of variance (MANOVA, 10000 permutations) was then performed to establish significant differences between species abundances between treatments and to test whether microclimate (predictor variables: mean temperature, mean maximum temperature, mean minimum temperature, mean air humidity, mean rainfall) had a significant influence on species distribution.

Vagrant species excluded from the analysis: Alopecosa cuneata (Clerck 1757), Enoplognatha thoracica (Hahn 1833), Euophrys frontalis (Walckenaer 1802), Evarcha falcata (Clerck 1757), Heliophanus flavipes (Hahn 1832), Malthonica silvestris (L. Koch 1872), Meta segmentata (Clerck 1757), Micaria fulgens (Walckenaer 1802), M. pulicaria (Sundevall 1831), Microlinyphia pusilla (Sundevall 1830), Philodromus albidus Kulczyn'ski 1911, Plururolithus minimus C.L. Koch 1839, Pisaura mirabilis (Clerck 1757), Steatoda phalerata (Panzer 1801), Tiso vagans (Blackwall 1834), Walckenaeria furcillata (Menge 1869), Xysticus kochi Thorell 1872, Zelotes subterraneus (C.L. Koch 1833).

RESULTS

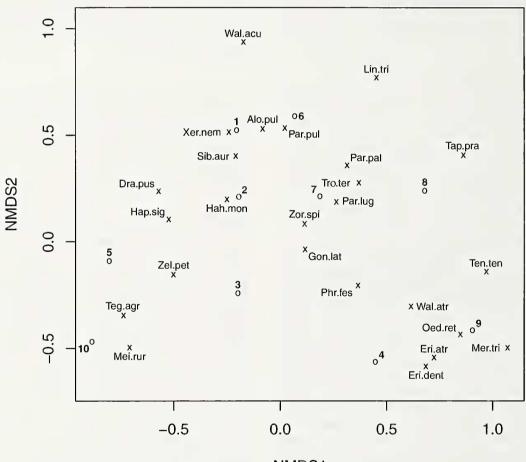
A total of 707 adult individuals belonging to 43 species and 357 juvenile spiders was captured. The most abundant species was Zelotes petrensis (C.L. Koch 1839) (n = 218), representing 32% of all caught specimens. Other frequent species were Erigone dentipalpis (Wider 1834) (n = 80), Xerolycosa nemoralis (Westring 1861) (n = 79), Tegenaria agrestis (Walckenaer 1802) (n = 50) and Erigone atra (Blackwall 1833) (n = 48).

Different treatments had significantly different microclimates. Mean temperature in drought plots was about 2.5° C and temperature maxima about 7° C higher than in control plots (Table 1). In contrast to this, mean temperature minima showed only a small difference between treatments. The mean air humidity was 10% lower in the drought plots that were totally protected from rain. Although these differences in microclimate between both treatments were significant, GLM indicated no significant effect either on number of species or on total counts of individuals (total, adult, juvenile) (Table 1). After ordination using non-metric multidimensional scaling (stress = 10.3) it was not possible to find any general groupings in species distribution between either treatment (Fig. 1). MANOVA showed no significant difference in assemblage composition of drought and control plots per se (P = 0.96). In accordance with this, a further MANOVA indicated no significant impact of any microclimate variable on species abundances (mean temperature: P = 0.32, mean temperature maxima: P = 0.66, mean temperature minima: P = 0.58, mean air humidity: P = 0.64, mean rainfall: P =0.20).

No changes in ecological traits were detected (Table 2). Moisture niche position was slightly higher in the drought plots (indicating lower preference for moisture) but differences were not significant. There was no increase in habitat specialization in the drought treatment, since moisture niche width did not differ significantly. Furthermore, the present

Table 1.—Main characteristics of drought and control plots: mean and standard deviation or median and 25% / 75%-quartiles (*) of captured spider species, individuals, adults, juveniles and microclimate (temp. = temperature, ampl. = amplitude). The differences were tested using GLM (*F*), *t*-test (*t*) or Wilcoxon rank test (*W*).

| Spiders | Drought plot $(n = 5)$ | Control plot $(n = 5)$ | Test result | | | |
|-----------------------|------------------------|------------------------|-------------|---------|----|---------|
| | | | F | Р | | |
| No. species | 17 (4) | 15 (5) | 0.14 | 0.71 | | |
| No. individuals | 111 (32) | 101 (33) | 0.19 | 0.67 | | |
| No. adults | 77 (26) | 64 (21) | 0.62 | 0.45 | | |
| No. juveniles | 34 (8) | 37 (15) | 0.13 | 0.73 | | |
| Microclimate | | | t | Р | W | Р |
| Temp. [° C] | 18.1 (0.1) | 15.6 (0.1) | 45.60 | < 0.001 | | |
| Temp. max [° C] | 30.9 (30.9/30.9)* | 23.9 (23.9/23.9)* | | | 25 | < 0.001 |
| Temp. min [° C] | 10.0 (9.9/10.4)* | 9.1 (9.1/9.7)* | | | 25 | < 0.05 |
| Day/night ampl. [° C] | 20.8 (0.3) | 14.6 (0.1) | 34.23 | < 0.001 | | |
| Air humidity [%] | 70 (0) | 80 (0) | | < 0.001 | | |
| Rain [mm] | 0 (0) | 42 (0) | | < 0.001 | | |



NMDS1

Figure 1.—Non-metric multidimensional scaling (NMDS) ordination (stress = 10.3) based on the Bray-Curtis dissimilarity matrix of spider species in drought (1–5) and control plots (6–10). Abbreviated species names: Alo-pul = *Alopecosa pulverulenta* (Clerck 1757), Dra-pus = *Drassylhus pusillus* (C.L. Koch 1833), Eri-atr = *Erigone atra* (Blackwall 1833), Eri-dent = *E. dentipalpis* (Wider 1834), Gon-lat = *Gongylidiellum latebricola* (O. Pickard-Cambridge 1871), Hah-mon = *Hahnia montana* (Blackwall 1841), Hap-sig = *Haplodrassus signifer* (C.L. Koch 1839), Lin-tri = *Linyphia triangularis* (Clerck 1757), Mei-rur = *Meioneta rurestris* (C.L. Koch 1836), Mer-tri = *Mermessus trilobatus* (Emerton 1882), Oed-ret = *Oedothorax retusus* (Westring 1851), Par-lug = *Pardosa lugubris* (Walckenaer 1802), Par-pal = *P. palustris* (Linnaeus 1758), Par-pul = *P. pullata* (Clerck 1757), Phr-fes = *Phrurolithus festivus* (C.L. Koch 1835), Sib-aur = *Sibianor aurocinctus* (Ohlert 1865), Tap-pra = *Tapinocyba praecox* (O. Pickard-Cambridge 1873), Teg-agr = *Tegenaria agrestis* (Walckenaer 1802), Ten-ten = *Tenuiphantes tenuis* (Blackwall 1852), Tro-ter = *Trochosa terricola* Thorell 1856, Wal-acu = *Walckenaeria acuminata* Blackwall 1833, Wal-atr = *Walckenaeria atrotibialis* O. P.-Cambridge 1878, Xer-nem = *Xerolycosa nemoralis* (Westring 1861), Zel-pet = *Zelotes petrensis* (C.L. Koch 1839), Zor-spi = *Zora spinimana* (Sundevall 1833).

| Ecological trait | Drought plot | Control plot | t | Р |
|-------------------------|------------------|------------------|-------|------|
| Moisture niche position | 0.456 ± 0.04 | 0.438 ± 0.04 | 0.697 | 0.51 |
| Moisture niche width | 0.177 ± 0.01 | 0.174 ± 0.01 | 0.495 | 0.63 |
| Body size [mm] | 4.81 ± 0.55 | 4.96 ± 0.62 | 0.396 | 0.70 |

Table 2.—Means (\pm SD) of ecological traits of spiders in the drought and control plots. The lower the values of moisture niche position the stronger the preference for moist habitats. Low values of niche width indicate a narrow niche (cf. Entling et al. 2007). Body size referred to the average body size of females. The differences were tested using *t*-tests.

results indicated that species were not on average larger in the drought plots.

DISCUSSION

The present experiment revealed no responses of spider fauna to altered drought at a small scale. Although microclimatic conditions in drought and control plots differed significantly, it was not possible to detect any differences in spider fauna. Neither the total species richness nor the activity densities of spider species and species composition differed between treatments. Furthermore, no significant changes in ecological traits (e.g., increasing habitat specialization) could be found.

There are several explanations for missing responses to changes in microclimate. First, the size of the plots could have been too small. Especially highly mobile spiders may be able to cope with unsuitable habitat conditions in a small area of 16 m^2 . On the other hand, Muff et al. (2009) showed that spider assemblages can change considerably within a few meters. Second, this study was planned to simulate a dry spell during the summer months, July to September, since changes in rainfall are expected to have the most significant effects. However, this study period could have been too short. Although the microclimate was significantly different in the drought plot, it may require more than three months until the soil is totally parched, especially because of the effect of dew formation at night. Nevertheless, one can conclude that a single drought period extending over three months had no significant impact on the spider fauna of dry grasslands and heathlands in the suboceanic climate region. As opposed to this, annual dry spells due to long-term climate change may indeed have an increasing impact on spider fauna. Lastly, the microclimatic conditions may not have been extreme enough to have an impact on spiders. Many species may have a wider ecological amplitude than assumed and thus be able to cope with higher temperatures and increasing drought than studied here.

Considering possible biases of the present experimental setup, further studies should last longer; for example, starting in May. Drought is expected to have a stronger impact during spring and early summer when precipitation is usually higher than in midsummer. On the other hand, spiders may be more influenced by drought during their breeding season; i.e., from April to June (cf. Tretzel 1954; Merrett 1967, 1968; Foelix 1996). Furthermore, larger shelters may be more suitable for detecting changes in speeies richness, abundance, composition or ecological traits in response to increasing drought. Lastly, it is strongly recommended to use a range of sampling techniques for further studies, including litter extraction (cf. Wagner et al. 2003), since responses of spider densities to changing microclimate seem to be more complex than what may be revealed by pitfall trapping alone. During this study, at least the small-bodied spiders were expected to respond to drought. Most of them are web-building species, such as Dictynidae, Linyphiidae or Theridiidae that have a small habitat size and thus might be influenced by changing microclimate. A general problem of this experiment may have been the use of only one sampling method. Several species may have responded to altered drought, but these responses were not detected by means of pitfall trapping. Pitfall trapping favors ground-dwelling spiders, but might be inappropriate for capturing species normally occurring in higher strata (Merrett & Snazell 1983; Harwood et al. 2001, 2003; Wagner et al. 2003).

Further investigations are necessary in order to understand the mechanisms underlying the responses of spiders in terms of species richness, community composition and ecological traits to microclimatic changes. Spiders were not a suitable model group to detect any changes during the present study. In contrast to this study, Frampton et al. (2000) and Lensing et al. (2005) observed effects of drought and altered precipitation on some spider families (e.g., Gnaphosidae). But, when comparing these results one have to keep in mind that all studies were conducted in habitat types providing totally different initial conditions (Frampton et al. 2000 - farmland, Lensing et al. 2005 - oak-maple forest, present study - dry grassland) that might determine the effect of changing microclimate (e.g., changes due to increased drought may be more drastic in humid than in dry habitats). However, comparable experiments yielded significant changes for microarthropods such as Collembola, Mesostigmata and Oribatida (Lindberg et al. 2002; Lensing et al. 2005). Within this context, Lindberg et al. (2002) outlined the suitability of oribatid mites as bioindicators, since oribatids have a low dispersal ability and low reproductive rates (MacLean et al. 1977; Hopkin 1997). In conclusion, for future small-scale studies I would recommend a multi-species group approach comprising micro- and macroarthropods using a broad spectrum of sampling techniques.

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